New Temnocephalans from the Branchial Chamber of Australian *Euastacus* and *Cherax* Crayfish Hosts

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Australian freshwater crayfish are hosts to ectosymbiotic, turbellarian worms of the temnocephalan subfamily Craspedellinae Baer, 1931 which are found in the the branchial chamber and are characterised by possession of one or more transverse papillate ridges across the dorsal body and crenulate (papillate) tentacles. The Craspedellinae is enlarged to accommodate four species viz. *Gelasinella powellorum* gen. et sp. nov. from *Euastacus spinifer* and three new species of *Craspedella* from *Cherax* spp. The definition of the Craspedellinae is emended to include a description of the organisation of the epidermal syncytial mosaic. The pattern of the epidermal syncytial mosaic of Craspedellinae is diagnostic for the subfamily, but not useful to discriminate either genera or species within the taxon. The biogeography of the Craspedellinae suggests an origin in Australia/New Guinea after the separation of South America and Australia from Antarctica (c. 45 mya) and coevolution and radiation with *Cherax* crayfish, followed by host switching to *Euastacus*.

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KEYWORDS: Australia, *Cherax*, *Craspedella*, Craspedellinae, crayfish, ectosymbionts, *Euastacus spinifer*, *Gelasinella*, Parastacidae, taxonomy, Temnocephalida.

INTRODUCTION

Australian crayfish are noted for their association with ectosymbiotic turbellarian worms, the Temnocephalida, of which one group, the Craspedellinae, are found in the branchial chamber. For more than 100 years *Craspedella spenceri* described by Haswell (1893) from the branchial chamber of the indeterminate Australian crayfish species, *Astacopsis bicarinatus* (= *Cherax* sp.), remained the only temnocephalan species recognised with papillate posterior dorsal ridges and the only described species in the genus. Recently Cannon and Sewell (1995) described a new genus *Heptacraspedella* from the crayfish *Euastacus bispinosus* from the Grampians, five new species of *Craspedella* from eastern Australian *Cherax* spp. crayfish and three new species in a new genus *Zygopella* from Western Australian *Cherax* spp. These temnocephalans which inhabit the branchial chamber of their respective hosts share a common facies of crenulate tentacles and dorsal posterior ridges. Cannon and Sewell (1995) recognised the subfamily Craspedellinae to include these three temnocephalan genera and predicted that further examination of Australian crayfish hosts would reveal a greater diversity for the subfamily. Moreover, they suggested that examination of large specimens of *Euastacus* may yield new species of gill-dwelling temnocephalans. Examination of the branchial chamber of *Euastacus spinifer* and *Cherax* spp. hosts as part of a Ph. D. study by KBS has revealed new taxa.

MATERIALS AND METHODS

Euastacus and *Cherax* crayfish were collected from freshwater habitats using baited collapsible minnow traps or occasionally by dip netting. To obtain temnocephalan worms, the carapace of crayfish was detached using strong forceps inserted anteriorly through the articular membrane and under the dorsal carapace, and the carapace and carcass were then placed into a shallow vessel containing filtered fresh water from the habitat. The inner surface of each branchiostegite (i.e. the branchiostegal membrane), the gills and the body wall were searched with the aid of a dissecting microscope. Worms were allowed to detach themselves spontaneously.

Worms for wholemounts were routinely fixed by flooding with hot (c. 90°C) 10% formalin buffered to pH 7.0 with phosphate (HF) for c. 30 s and then transferred to 10% phosphate buffered formalin (Form.) at ambient room temperature. Worms were then rinsed in distilled water, stained with either Mayer's or Harris's Haematoxylin (Hx), dehydrated in ethanol, cleared in xylene and mounted in Canada balsam. Worms for serial sections were fixed in either Bouin's fluid (Bouin) or Form. at ambient room temperature, dehydrated in ethanol, embedded in 'Paraplast' at 56°C, sectioned at 4–7 m and stained with Mayer's Haematoxylin and eosin (H&E), cleared and mounted in Depex.

To show the epidermal mosaic, live temnocephalans were fixed by flooding with a solution of 2% silver nitrate heated to c. 60°C, washed in distilled water then exposed to either bright sunlight or incident light from a Volpi 'cold light' source for c. 15–30 min, dehydrated in ethanol and mounted in Euparol. For scanning electron microscopy (SEM) specimens were fixed by flooding with HF, washed for 30 s to remove surface contamination in a 20% solution of Decon 90 detergent and rinsed c. six times in filtered distilled water. Worms were then dehydrated in ethanol, critical point dried, mounted on stubs, coated with gold, and examined with a Hitachi S–530 SEM operating at 25 kilovolts. Photographs for figures were scanned from 35 mm negative film onto Kodak *PhotoCD*™ and edited, then assembled into plates using Adobe *Photoshop*™. Lineart illustrations for figures were prepared using Adobe *Illustrator*™ from templates of scanned sketches prepared by pen and ink with the aid of a drawing tube.

Terminology and Measurements

Descriptive terminology essentially follows the conventions established by Cannon and Sewell (1995). The term vesicula resorbiens used in error by Cannon and Sewell (1995) is corrected to vesicula resorbens (see Cannon 1993). Names for the syncytia which comprise the epidermal mosaic follow those established by Joffe et al. (1995a, b). Taxonomic material is deposited in the collections of the Queensland Museum (QM) and specimen slide preparations are designated as either: wholemount (WM); de Faure's mounting medium (deF) (see Evans, Sheals and MacFarlane (1961) for recipe details) cirrus preparation (CP); longitudinal serial section (LS); oblique serial section (OS): the number of slides in the registered series is given in square brackets. Specimen data for QM registered material examined is listed in the order: registration number; specimen/slide preparation details (in parentheses); location on host; host scientific name; locality details; date collected; collector(s); histological fixation/staining procedures. Where the crayfish host was collected by those other than the collector of the worms the labelling convention — host collector name/worm collector name — is observed. Full registration details are provided for each holotype specimen. For all subsequent specimens listed in the material examined, the QM registration number and specimen/slide preparation details are provided, ***followed by only those data which are different from that of the preceding registration***. For clarity, discrete blocks of registration data are separated by semi-colons.

Terminology applied to the male copulatory organ is derived from Cannon and Sewell (1995). In addition, the arrangement and orientation of the spined ridges of the cirrus introvert is characterised as approximately either parallel or diagonal in relation to

the longitudinal axis of the inverted introvert. Descriptions of the cirrus refer to the inverted state of the organ and exclude fine details of the introvert spines. The measurements provided for soft structures and the cirrus are taken only from the worms which comprise respectively the taxonomic type series [WM, LS and OS] and CP series unless otherwise stated, for example, the seminal receptacle was rarely discernable in WM. All taxonomic measurements were made with the aid of a drawing tube and are presented in μm as a range followed usually by the mean in parentheses. Where no range is provided the measurements were the same for all worms, and where measurements are only approximate they are preceded by the qualifier c.

For measurement of the cirrus, live worms were placed on a microscope slide in a drop of filtered fresh water then passed over a flame for a few seconds to heat the water and kill the specimen in an extended position. After fixation in hot water (HW) by this method, excess water was removed by pipette, a drop of deF added, and the specimen covered with a coverslip. Cirrus dimensions were measured as described previously by Cannon and Sewell (1995) on drawing tube drawings using a metal ruler for straight dimensions and a map measure (Western-Germany) for curved dimensions. The registration number of any voucher specimens of host crayfish lodged in the QM Crustacean collection is provided.

SYSTEMATICS

Gelasinella gen. nov.

Diagnosis

Craspedellinae with two posterior, dorsal, low, transverse papillate ridges and posteriorally four short ridges consisting of raised points radiating towards the posterior body margin. The most posterior transverse ridge has a slight central indentation.

Type species

Gelasinella powellorum sp. nov.

Etymology

Latin, *gelasinus*, dimple (masculine), a reference to the central indentation on the most posterior dorsal transverse ridge.

Remarks

The number and form of the dorsal ridges differ from those of other members of the Craspedellinae described by Cannon and Sewell (1995). The exact configuration of the transverse and posterior ridges was only possible to determine using SEM, although the central indentation was clearly observed on live worms, wholemounts and silver nitrate stained preparations (Fig. 1). The SEM also revealed a semi-regular, transverse line of large multiciliated papillae distal to the most anterior transverse dorsal ridge which were not raised on a dorsal ridge (Fig. 1).

Gelasinella powellorum sp. nov.
(Figs 1; 2A, B; 3A)

Material examined

Holotype: QMGL18659 (WM), ex branchial chamber *Euastacus spinifer* from Mammy Johnsons River (tributary of Karuah River), NSW (32°19′S; 151°57′E) 31/Aug/1995 Powell J. and Powell R./Sewell K.B. HF/Hx.

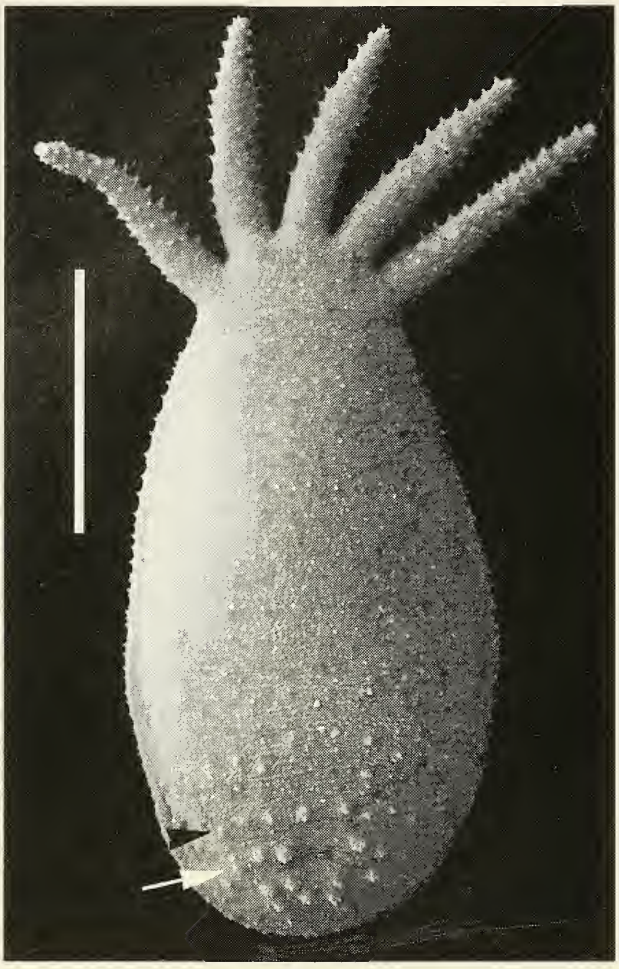

Figure 1. Scanning electron micrograph of *Gelasinella powellorum* gen. et sp. nov. from the type locality fixed in HF and shown in dorsal view. The most anterior of the two dorsal ridges (arrowhead) is continuous across the body. The posterior dorsal ridge (arrow) has a central indentation or 'dimple' from which papillae are absent. Scale = 200 μm.

Paratypes: QMGL18660–18661 (WM); QMGL18666 (LS[1]) Bouin/H&E.

Other material: QMGL18662–18663 (WM) HF/Hx; QMGL18667 (LS[1]) Bouin/H&E; QMGL18669 cirrus inverted (CP[6]) HW/deF; QMGL18664–18665 (WM), from Karuah River at Washpool Bridge, NSW (32°21′S; 151°55′E) 28/Aug/1995 Powell J. and Powell R./Sewell K.B. HF/Hx; QMGL18668 cirrus part everted (CP[6]) HW/deF; QMGL18675 (LS[1]) Bouin/H&E.

Description

External

Body from posterior margin to tip of tentacles 607–667 (647), to eyes 409–442 (424) long and 266–270 (268) wide. Posterior disc 145–172 (156) in diameter; peduncle 87–100 (93) in diameter. Epidermis c. 2–3 high dorsally and ventrally.

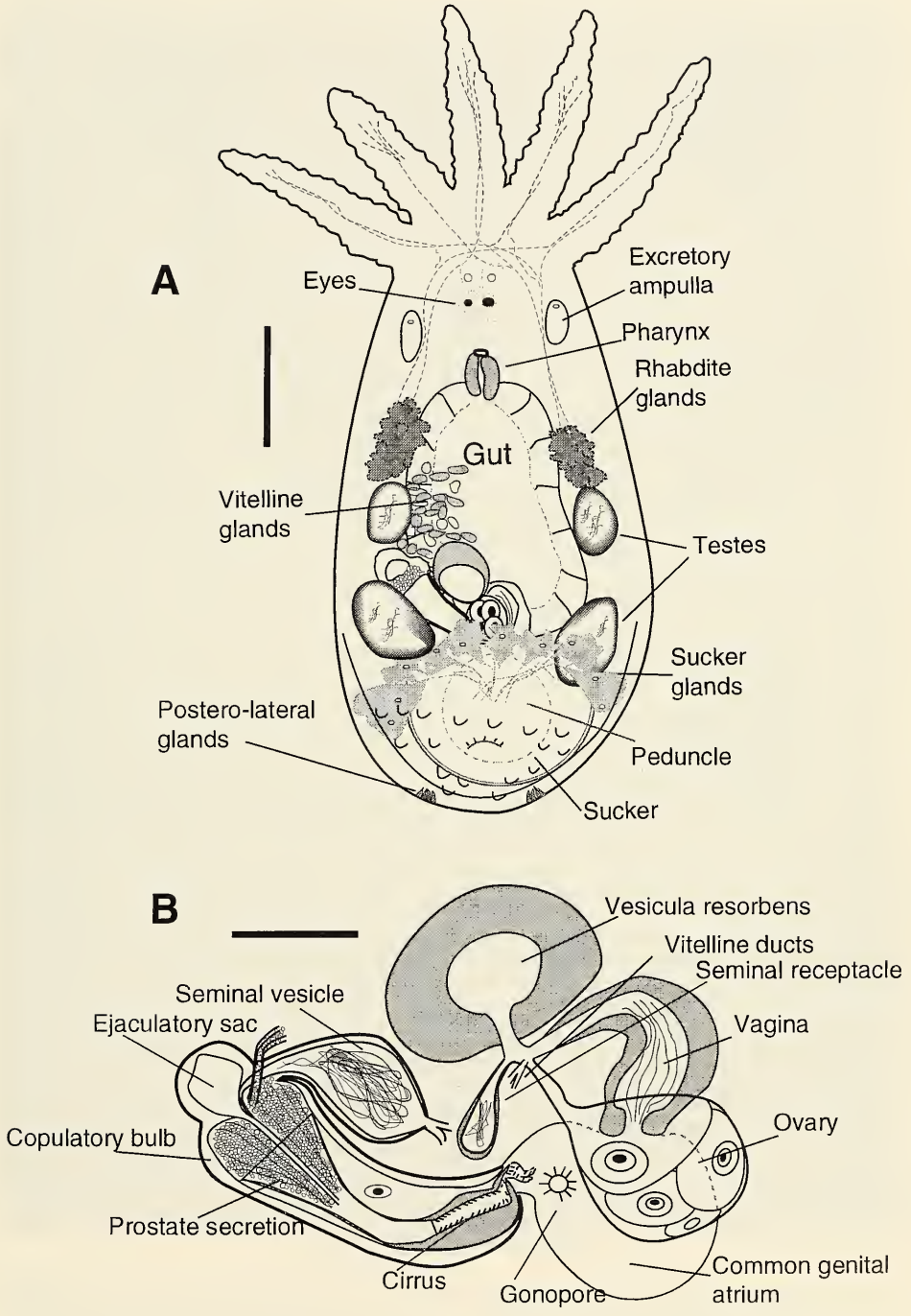

Figure 2. Gelasinella powellorum gen. et sp. nov. (A) = Holotype QMGL18659 in dorsal view. Scale = 100 μm, (B) = Reproductive structures from live specimen in dorsal view. Scale = 50 μm.

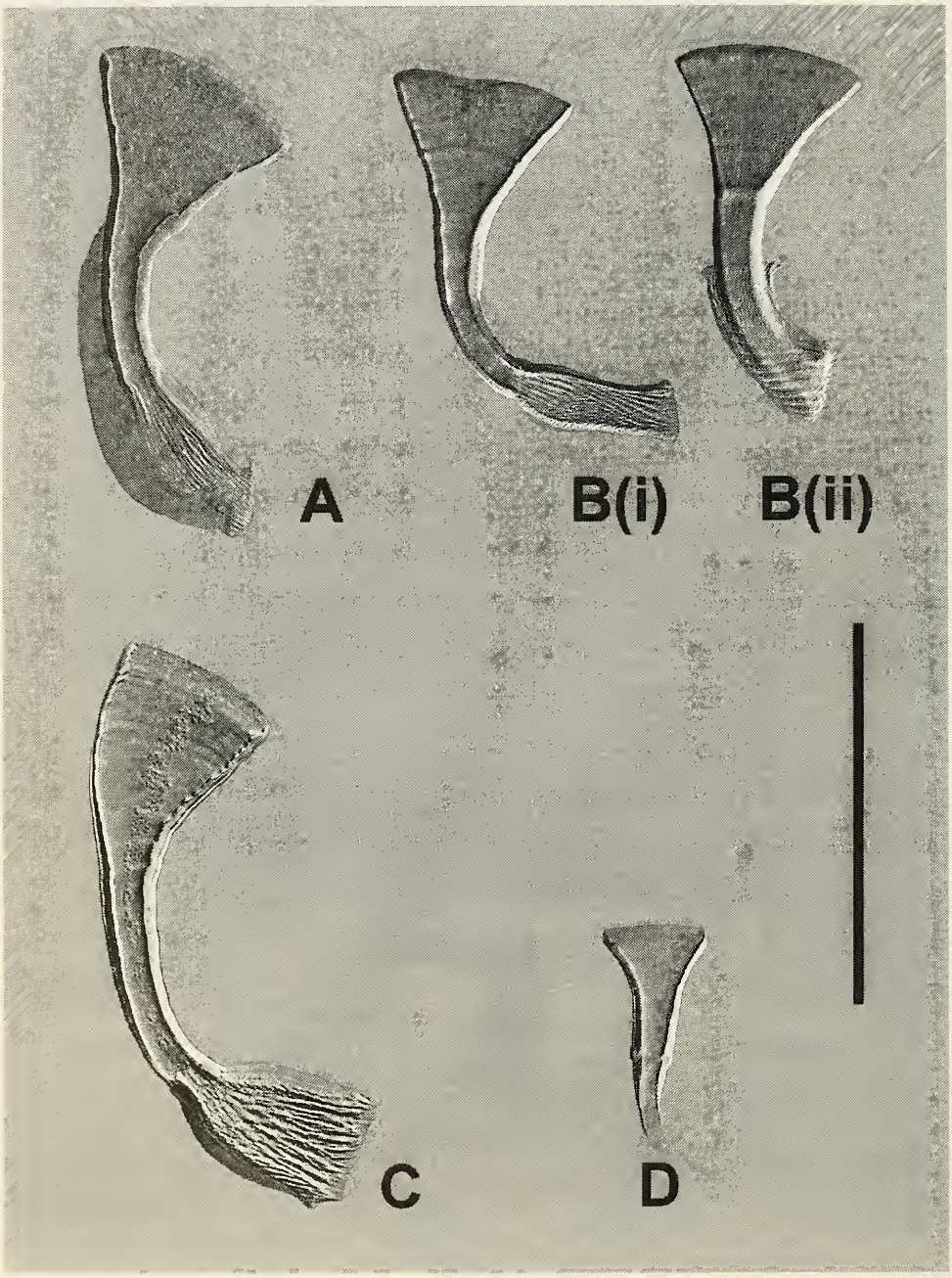

Figure 3. Nomarski interference photomicrographs of cirri of adult worms from the type host and locality. Scale = 100 μm, (A) = *Gelasinella powellorum* gen. et sp. nov., inverted. Note: the introvert swelling is unusually obvious for this particular specimen of the species; and the distal region of the introvert is typically constricted and reflexed, (B) = *Craspedella bribiensis* sp. nov., (i) inverted, (ii) everted, (C) = *Craspedella cooranensis* sp. nov., inverted, (D) = *Craspedella joffei* sp. nov., inverted.

General Anatomy

Pharynx 37–45 (41) long, 24–28 (27) wide. Gastrodermis c. 25–40 high. Excretory ampullae 39–45 (43) long and 22–31 (27) wide. Eyes c. 11 across. Posterior glands present and discharging from two postero-lateral regions.

Reproductive System. Female

Ovary 33–41 (37) long, 30–34 (31) wide. Vesicula resorbens 47–58 (54) long, 42–55 (47) wide, wall c. 3–10 thick. Seminal receptacle c. 60 long, 15 wide (from live worms).

Reproductive System. Male

Anterior testes 62–81 (67) long, 39–62 (48) wide. Posterior testes 67–81 (78) long, 45–67 (59) wide. Seminal vesicle 56–66 (62) long, 27–31 (30) wide. Copulatory bulb 36–41 (38) long, 39–44 (42) wide, with semi-discrete ejaculatory sac. Prostate duct reservoirs parallel. Cirrus (based on 6 part-everted adult specimens ex QMGL18668) 153–167 (160) long in total. Shaft cone-shaped, curved; proximal opening 43–57 (54) wide, with narrow or thickened rim. Introvert with constricted and reflexed distal region, 11–12 (11) wide at base, longer side 72–80 (76) long, shorter side 39–41 (40) long (i.e. introvert c. 4 times longer than width of introvert base), with asymmetrical swelling i.e. longer side much wider and extending proximally well past the base of the introvert, distal opening c. 15 wide. Rows of inverted spines, except for those in the reflexed distal region, oriented parallel to long axis of the introvert.

Hosts

Euastacus spinifer: Parastacidae.

Locality

Karuah River system, NSW.

Etymology

For both Robyn Powell and her husband Jules who provided the host from which the first specimen was recognised.

Remarks

The cirrus of this species has a distinctive form when alive, as the distal region of the inverted introvert is reflexed and the region immediately proximal to the everted region is constricted (Figs 2B, 3A). This makes the exact form and dimensions of the distal region of the inverted introvert difficult to determine. The introvert is revealed clearly however when everted to have the form of the typical cirri of the Craspedellinae. Measurements of introvert length were all derived from partially everted cirri. The swelling on the longer side of the introvert extends proximally further past the introvert base than in any other species in the Craspedellinae. The ejaculatory sac of this species is more discrete than in any other species of Craspedellinae (Fig. 2B). Host voucher specimen QMW20765.

Craspedella Haswell, 1893

Diagnosis

Craspedellinae with three dorsal papillate ridges in the posterior half of the body and, behind the last ridge, four short posterior papillate ridges radiating towards the posterior body margin.

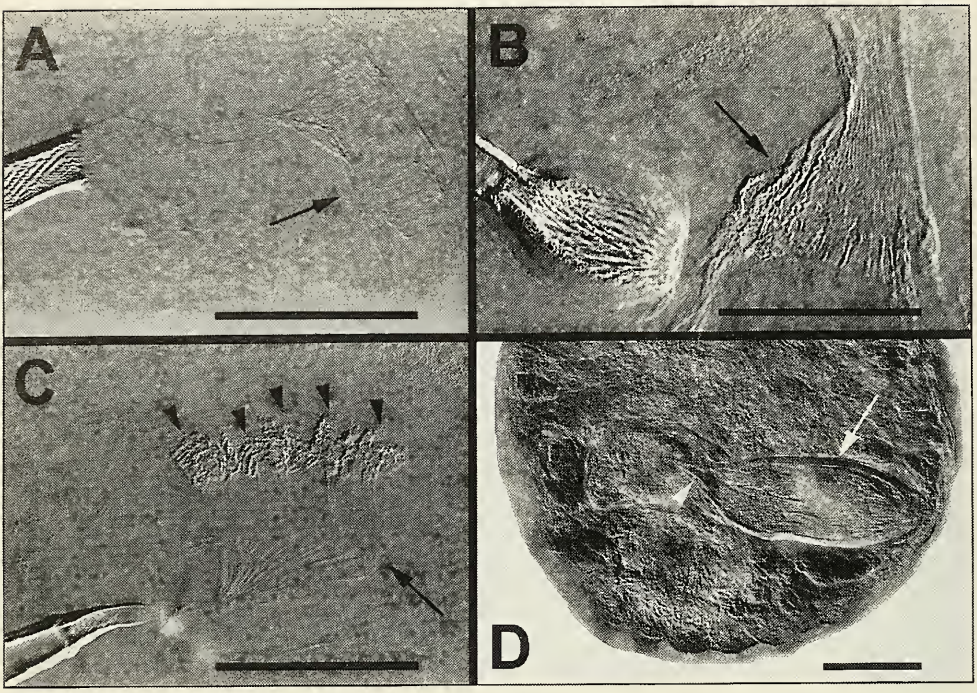

Figure 4. (A) = Nomarski interference micrograph of the distal tip of the cirrus and the vagina of *Craspedella bribiensis* sp. nov. cleared in deF to reveal the shape of the vaginal cavity (arrow). Scale = 50 μm, (B) = Nomarski interference micrograph of the distal tip of the cirrus and the vagina of *C. cooranensis* sp. nov. cleared in deF to reveal the shape of the vaginal cavity (arrow). Note the introvert swelling is unusually obvious for this particular specimen of the species. Scale = 50 μm, (C) = Nomarski interference micrograph of the distal tip of the cirrus and the vagina of *Craspedella joffei* sp. nov. cleared in deF to reveal the shape of the vaginal cavity (arrow) and the unique distal 'pockets' (arrowheads). Scale = 50 μm, (D) = Light micrograph of the posterior end of *Craspedella joffei* sp. nov. QMGL18654 in dorsal view stained in H&E showing the large size of the copulatory bulb (arrow) relative to the size of the cirrus (arrowhead). Note the lack of an ejaculatory sac. Scale = 50 μm.

Type species

Craspedella spenceri Haswell, 1893

Other species

Craspedella bribiensis sp. nov.; *C. cooranensis* sp.nov.; *C. gracilis* Cannon and Sewell, 1995; *C. joffei* sp. nov.; *C. pedum* Cannon and Sewell, 1995; *C. shorti* Cannon and Sewell, 1995; *C. simulator* Cannon and Sewell, 1995; *C. yabba* Cannon and Sewell, 1995

Craspedella bribiensis sp. nov.
(Fig. 3Bi-ii; 4A)

Material examined

Holotype: QMGL18627 (WM) ex branchial chamber *Cherax robustus* from Bribie Island, pool beside McMahon Road, Qld, Australia (27°02.5′S; 153°10.3′E) 31/Jan/1995 Sewell K.B., Cannon L.R.G., Khalil Z. and Short J. HF/Hx.

Paratypes: QMGL18628–18629 (WM); QMGL18631 (LS[1]) Bouin/H&E.

Other material: QMGL18630 (WM) HF/Hx; QMGL18632 (WM); QMGL18633 (OS/LS[1]) Bouin/H&E; QMGL18634 (LS[1]); QMGL18635 cirrus inverted (CP[6], 6 adult specimens) HW/deF; QMGL18636 cirrus everted (CP[6], 6 adult specimens).

Description

External

Body from posterior margin to tip of tentacles 638–667 (654), to eyes 428–437 (431) long and 230–274 (256) wide. Posterior disc 120–145 (132) diameter; peduncle 77–80 (79) diameter. Transverse body ridges do not form lamellae. Epidermis c. 2 high dorsally and ventrally.

General Anatomy

Pharynx 30–34 (32) long, 25–30 (28) wide. Gastrodermis c. 25 high. Excretory ampullae 45–53 (50) long, 28–34 (31) wide. Eyes c. 11 across.

Reproductive System. Female

Ovary 31–50 (41) long, 23–44 (35) wide. Vesicular resorbens 56–69 (61) long, 44–59 (49) wide, wall c. 3–11 thick. Seminal receptacle c. 30 long, 15 wide (from live worms).

Reproductive System. Male

Anterior testes c. 50–81 (62) long, 39–75 (52) wide. Posterior testes c. 66–94 (80) long and 41–86 (62) wide. Seminal vesicle 53–69 (60) long, 27–30 (28) wide. Copulatory bulb 34–36 (35) long, 39–44 (41) wide, with ejaculatory sac. Prostate duct reservoirs parallel. Cirrus (based on 6 fully inverted adult specimens ex QMGL18635) 138–145 (141) long in total. Shaft narrow, funnel-shaped, curved, thick-walled, with distal region less than length of introvert; proximal opening 35–48 (41) wide, with narrow rim. Introvert slightly curved, 8–10 (9) wide at base, longer side 46–53 (49) long, shorter side 41–44 (42) long (i.e. introvert c. 5.5 times longer than width of introvert base), with narrow swelling slightly wider on longer side, distal opening 12–15 (14) wide. Rows of inverted spines oriented obliquely to long axis of the introvert.

Hosts

Cherax robustus: Parastacidae.

Locality

Bribie Island, south-east Qld.

Etymology

From Bribie, referring to the type locality, the area of Bribie Island.

Remarks

The prominent and oblique rows of spines on the inverted introvert distinguish this species clearly from *C. simulator* (see Cannon and Sewell 1995: 407, Fig. 3Ei–iii), which it otherwise resembles closely (Fig. 3Bi-ii).

Craspedella cooranensis sp. nov.
(Figs 3C; 4B)

Material examined

Holotype: QMGL18637 (WM) ex branchial chamber *Cherax depressus* from Mt. Mothar foothills, creek crossing Shadbolt Road, Qld, Australia (26°13.6′S; 152°46.3′E) 8/Nov/1995 Sewell K.B. and Short J. HF/Hx.

Paratypes: QMGL18638–18639 (WM); QMGL18640–18641 (LS[1,1]) Bouin/H&E.

Other material: QMGL18642 (OS[1]) Bouin/H&E; QMGL18643 cirrus inverted (CP[6], 6 adult specimens) HW/deF; QMGL18644 cirrus everted (CP[1], 1 adult specimen).

Description

External

Body from posterior margin to tip of tentacles 563–594(575), to eyes 374–415 (393) long and 164–296 (242) wide. Posterior disc 119–164 (149) diameter; peduncle 94–129 (109) diameter. Transverse body ridges do not form lamellae. Epidermis c. 2 high dorsally and ventrally.

General Anatomy

Pharynx 30–37 (33) long, 22–31 (28) wide. Gastrodermis c. 25 high. Excretory ampullae 42–56 (51) long, 22–31 (28) wide. Eyes c. 14 across.

Reproductive System. Female

Ovary 37–47 (42) long, 28–34 (32) wide. Vesicular resorbens 62–114 (80) long, 44–75 (55) wide, wall c. 3–10 thick. Seminal receptacle c. 19 long, 9 wide.

Reproductive System. Male

Anterior testes 39–67 (53) long, 34–47 (40) wide. Posterior testes c. 58–87 (73) long and 34–67 (47) wide. Seminal vesicle 75–97 (84) long, 30–34 (32) wide. Copulatory bulb 39–42 (40) long, 36–41 (38) wide, with ejaculatory sac. Prostate duct reservoirs parallel. Cirrus (based on 6 fully inverted adult specimens ex QMGL18643) 148–169 (161) long in total. Shaft narrow, goblet-shaped, curved, thick-walled, with distal region greater than length of introvert; proximal opening 43–59 (51) wide, with narrow rim. Introvert not curved, 10–12 (11) wide at base, longer side 47–48 (48) long, shorter side 41–45 (43) long (i.e. introvert c. 4.5 times longer than width of introvert base), with wide symmetrical swelling, distal opening 19–29 (25) wide. Rows of inverted spines oriented parallel to long axis of the introvert.

Hosts

Cherax depressus complex sensu Riek, 1951: Parastacidae.

Locality

Cooran Tableland, south-east Qld.

Etymology

From Cooran which refers to the type locality; the area of the Cooran Tableland.

Remarks

The extremely wide distal opening and the almost symmetrical shape of the cirrus introvert serve to distinguish clearly the species from *Craspedella bribiensis* (Figs 3Bi-ii;

4A) and *C. simulator* (see Cannon and Sewell 1995: 407, Fig. 3Ei-iii), which have an otherwise similar general anatomy and morphology (Figs 3C; 4B). The host, although presently referable to *Cherax depressus*, appears to be part of a species complex in need of taxonomic revision (John Short, Crustacea Section, QM, pers. comm.). Host voucher specimen QMW22257.

Craspedella joffei sp. nov.
(Figs 3D; 4C, D)

Material examined

Holotype: QMGL18645 (WM) ex branchial chamber *Cherax punctatus* from Mt. Mothar foothills, Shadbolt and Hartwig Road junction, Qld, Australia (26°13.8′S; 152°46.3′E) 26/Feb/1995 Sewell K.B., Sewell S.G., Sewell R.D. and Sewell M.R. HF/Hx.

Paratypes: QMGL18646 (WM); QMGL18648 (WM); QMGL18649–18650 (LS[1,1]) Bouin/H&E.

Other material: QMGL18647 (WM) HF/Hx; QMGL18651–18652 (WM); QMGL18658 cirrus inverted (CP[7]), 8 adult specimens, HW/deF; QMGL18653–18654 (WM) 21/Jul/1994 Short J. and Humpherys A./Sewell K.B. Form./Hx; QMGL18656–18657 (LS[1]) H&E; GL18897 (LS [1,1] Dingo Creek, near Traveston (26°19′S; 152°47′E) Mar/1973 Monteith G.B. Bouin/H&E.

Description

External

Body from posterior margin to tip of tentacles 733–771 (749), to eyes 461–503 (481) long and 217–230 (222) wide. Posterior disc 120–131 (125) diameter; peduncle 69–70 (69) diameter. Transverse body ridges do not form lamellae. Epidermis c. 2 high dorsally and ventrally.

General Anatomy

Pharynx 37–45 (42) long, 27–36 (31) wide. Gastrodermis c. 30 high. Excretory ampullae 52–59 (55) long, 23–45 (32) wide. Eyes c. 12 across. Posterior glands present and discharging into two postero-lateral regions.

Reproductive System. Female

Ovary 50–55 (53) long, 39–42 (41) wide. Vesicula resorbens 95–116 (103) long, 77–84 (80) wide, wall c. 3–10 thick. Seminal receptacle c. 20 long, 10 wide (from live worms). Vagina with wide proximal region composed of numerous pockets (c. 10) (Fig. 4C), outer musculature relatively very strong.

Reproductive System. Male

Anterior testes 44–57 (50) long, 34–39 (38) wide. Posterior testes 75–86 (81) long and 36–53 (41) wide. Seminal vesicle muscles extremely strong 89–98 (94) long, 39–45 (43) wide. Copulatory bulb muscles extremely strong, 141–153 (146) long, 66–73 (69) wide, without ejaculatory sac. Prostate duct reservoirs parallel. Cirrus (based on 8 adult specimens ex QMGL18658) 54–63 (57) long in total. Shaft cone-shaped, not curved, thick-walled; proximal opening 22–33 (27) wide, with thick rim. Introvert slightly curved, 6–6 (6) wide at base, longer side 20–22 (22) long, shorter side 18–20 (19) long (i.e. introvert c. 3.5 times longer than width of introvert base), with symmetrical swelling thick only in region of base of introvert, distal opening 3–4 (4) wide. Rows of inverted spines oriented parallel to long axis of the introvert.

Hosts

Cherax punctatus: Parastacidae.

Locality

Cooran Tableland, southeast Qld.

Etymology

For Dr Boris Joffe who first drew our attention to a live specimen of this species.

Remarks

The anatomy and morphology of the male and female reproductive system is unique and serves to distinguish the species clearly. The cirrus is tiny and the copulatory bulb large compared with those of any other species in the genus except *C. shorti* which has a typical cirrus for the genus but has a large copulatory bulb (Cannon and Sewell 1995) (Fig. 4D). Other similarities exist between *C. joffei* sp. nov. and *C. shorti*: they are the only species of *Craspedella* which lack an ejaculatory sac and possess postero-lateral glands similar to those of *Temnocephala minor* (see Cannon and Watson 1996). In live *C. joffei* sp. nov., the numerous pockets in the proximal region of the vagina were observed to expand in concert by muscle action and to thus increase markedly the internal proximal volume of this region of the vagina (Fig. 4C). Reproductive adaptations such as this could relate to adaption of the crayfish host *Cherax punctatus* to dry environments (John Short, Crustacea Section, QM, pers. comm.). The large internal volume of the vagina of *Craspedella joffei* sp. nov. either could accommodate a large quantity of copulatory secretions available potentially from the enormous copulatory bulb, or it may relate to the speed of formation of eggs. The size of the eggs of *C. joffei* sp. nov. are, however, no larger than those of other Craspedellinae (KBS, unpublished observations). Host voucher specimen QMW19930.

Epidermal mosaic

The epidermis of all species of Craspedellinae described in the present study and previously by Cannon and Sewell (1995) is multisyncytial and composed of five syncytia which together comprise the epidermal mosaic: the frontal; post-tentacular; trunk; stalk; and adhesive disc syncytium. Fig. 5 presents the features and organisation of the mosiac. None of the syncytia are 'paired syncytia' sensu Joffe et al. (1995a, b). The frontal syncytium covers the tentacles and is delineated on the ventral surface by the anterior border of the trunk syncytium and dorsally by the anterior border of the post-tentacular syncytium. The post-tentacular syncytium is 'saddle-shaped' (after Williams 1982) and does not contain the nephridiopores. The trunk syncytium covers the entire dorsal body posterior to the posterior border of the post-tentacular syncytium and the ventral body posterior to the frontal syncytium excluding the stalk syncytium. The trunk syncytium is tubular and encompasses ventrally the mouth and gonopore and dorsally the nephridiopores. The stalk syncytium circumscribes the ventral insertion of the peduncle into the body and covers the peduncle and the dorsal region of the disc of the posterior attachment organ. The peduncle insertion is circumscribed closely by the anterior border of the stalk syncytium but the posterior border of the stalk syncytium extends out to close to the posterior margin of the body. The adhesive disc syncytium covers the ventral surface of the disc but not the 'marginal valve' sensu Sewell and Whittington (1995).

Since this pattern has been found consistently in all members of the Craspedellinae (see, for example, Sewell and Cannon (1995): 153, Fig. 1), we propose that the subfami-

ly diagnosis presented by Cannon and Sewell (1995) be emended to include the following details of the epidermal mosaic:

Craspedellinae Baer, 1931

Epidermis composed of five 'unpaired' epidermal syncytia: frontal; post-tentacular; trunk; stalk and adhesive disc syncytium. Post-tentacular syncytium elongate-oval in shape, confined to the dorsal surface and bordered anteriorally by the frontal syncytium and posteriorally by the trunk syncytium. Nephridiopores positioned laterally in the dorsal trunk syncytia and just posterior to the posterior border of the post-tentacular syncytium. Border between the trunk and stalk syncytia confined to the ventral surface and circumscribing the insertion of the peduncle closely anteriorly and widening posteriorly to follow the posterior margin of the body.

DISCUSSION

Apart from the almost ubiquitous external temnocephalans, first reported from *Euastacus* crayfish by Haswell (1893), we must now recognise that *Euastacus,* like

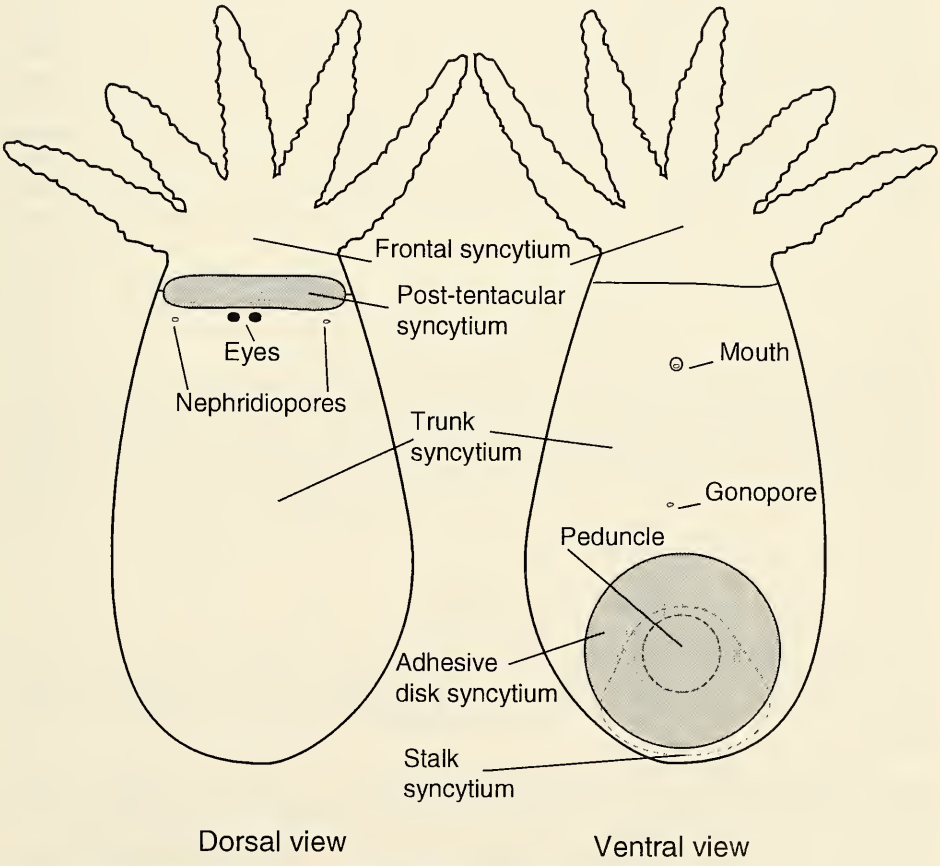

Figure 5. The organisation of the epidermal syncytial mosaic in Craspedellinae.

Cherax, are hosts to members of the gill-dwelling Craspedellinae. The subfamily Craspedellinae, as defined by Cannon and Sewell (1995), is expanded to include three new species of *Craspedella* and a single species from a new genus, *Gelasinella,* and emended to include details of the epidermal mosaic. The Craspedellinae now contains four genera with a total of 14 species of temnocephalans, all from the branchial chamber of crayfish, and characterised by possession of crenulate tentacles and one or more transverse dorsal papillate ridges. The well-developed dorsal ridges and the regular arrangement of prominent papillae on the body and tentacles provides this taxon with a distinctive facies.

The organisation of the epidermal mosaic for the Craspedellinae is included here for the first time in a taxonomic description of any temnocephalan. The potential of the pattern of the epidermal mosaic as a taxonomic character within the Temnocephalidae was heralded by Sewell and Cannon (1995) who observed differences between the pattern they observed for *Craspedella pedum* and that figured for species of *Temnocephala* by Williams (1982, 1992). The significance of the epidermal mosaic for the classification of temnocephalans was extended to the ordinal level in studies by Joffe et al. (1995a, b) and is the subject of ongoing study by Dr Boris Joffe (Zoological Institute, St Petersburg, Russia) and his colleagues.

The biogeography of the Craspedellinae matches that of *Cherax* crayfish which implies the worms coevolved and radiated with these crayfish. Two monotypic genera of Craspedellinae, *Heptacraspedella* containing *H. peratus* and *Gelasinella* containing *G. powellorum*, are now described from *Euastacus* crayfish in mainland Australia. Evidence from the biogeography suggests that these worms on *Euastacus* have 'host switched' from *Cherax*. Changing climate over geological time, particularly an increase in temperature and drying during the Tertiary period (from 65 mya), has led to habitat restriction of *Euastacus* crayfish in north and mid-eastern Queensland. *Euastacus* now exist only as isolated 'relic' populations in cool, forested, wet highland areas (>800 m elevation), whereas in lower latitudes, they occur at sea level (Morgan 1988, 1991; Horwitz 1990; Short and Davie 1993; Cannon and Sewell 1994). By contrast, few Australian species of *Cherax* [a genus restricted to mainland Australia, southern New Guinea including the Aru Islands and Misool [Palau I.] (Reik 1969, 1972; Banarescu 1990; Short and Davie 1993)], are endemic to wet upland or highland areas: the crayfish are found commonly in slower, lowland or coastal streams and in the foothills of uplands, often (but not always) with open canopy above (Riek 1969; Short and Davie 1993; Cannon and Sewell 1995). In north and mid-eastern Queensland, populations of *Cherax* and *Euastacus* are separated by pronounced physical barriers and, with the single known exception of *Cherax parvus* which occurs sympatrically with *Euastacus yigara* in the Tully River catchment (at an altitude of c. 750 m), are clearly discrete (Morgan 1988,1991; Horwitz 1990; Short and Davie 1993). As latitude increases, however, *Euastacus* are less confined to high altitude, and in southern Australia, suitable habitat for *Euastacus* occurs down to sea level (Morgan 1988; Cannon and Sewell 1994). Thus, in southern Australia there exists potentially more opportunity for ectosymbiotic worms such as the Craspedellinae to 'host switch' between *Cherax* and *Euastacus* crayfish. Of the two species of Craspedellinae known to infect *Euastacus*, i.e. *Gelasinella powellorum* and *Heptacraspedella peratus*, both occur at moderately high latitudes, in mid-eastern NSW, and in the Grampians region, respectively. In the Grampians, which is the type locality of *H. peratus*, both *Euastacus* and *Cherax* were reported by Riek (1972) to co-inhabit streams.

The depauperate distribution of Craspedellinae on *Euastacus* and particularly their apparent absence from the 'relic' Queensland populations of the genus suggests that the Craspedellinae have not radiated with these hosts although the possibility of extinctions in *Euastacus* populations cannot be excluded. Cannon and Sewell (1995) proposed that the Craspedellinae may not be detected in populations of *Euastacus* if only small cray-

fish were examined. They suggested this to be the reason that Craspedellinae were not found in their samples of mainly small *Euastacus* collected from Cape York to the Grampians. This argument is not supported, however, by data from the Karuah River region, NSW. On 21/Nov/1996, KBS and Dr Robert D. Adlard found numerous *Gelasinella powellorum* on a small juvenile (25 mm occipital carapace length (OCL)) as well as on a large adult (83 mm OCL) specimen of *Euastacus spinifer* collected from Mammy Johnsons Creek, just south-east of Stroud Road township, NSW (32°20.57′S; 151°56.11′E).

Queensland species of *Euastacus* do not appear to be hosts to Craspedellinae: none of 13 Queensland populations of *Euastacus*, including six 'relic' ones, examined for temnocephalans during the course of fieldwork by Cannon and Sewell (1994), was infected with Craspedellinae and examination of small and large specimens collected subsequently from southern and northern Queensland also failed to reveal any species. The Craspedellinae thus probably have radiated with *Cherax* as their hosts and have transferred subsequently to *Euastacus* only in southern regions where the host genera may/can occur sympatrically. It is pertinent to note, however, that *E. yigara* and *C. parvus*, which occur sympatrically in northern Queensland, have not yet been examined for Craspedellinae.

Craspedellinae are unknown from Tasmanian parastacids. Craspedellinae were not reported from any Tasmanian crayfish by either Haswell (1893) or Hickman (1967), nor have they been detected subsequently (Cannon and Sewell unpublished observations). The absence of the worms is consistent with the fact that neither *Cherax* nor *Euastacus* occur in Tasmania (Riek 1969; Holthuis 1982). *Euastacus* also are absent from Papua New Guinea, although numerous species of *Cherax* are recorded there (Holthuis 1949, 1982). Therefore, the report of a putative species of Craspedellinae from *Cherax communis* in Papua New Guinea by Cannon and Sewell (1995), further supports the hypothesis that the Craspedellinae have radiated with *Cherax*. The biogeographical distribution of the Craspedellinae is consistent with an origin in Australia/New Guinea after the separation of South America and Australia from Antarctica (c.45mya).

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